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SOME CERVID TEETH FROM THE TUNG GUR FORMATION OF MONGOLIA, AND ADDITIONAL NOTES ON THE GENERA *STEPHANOCEMAS* AND *LAGOMERYX*¹

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INTRODUCTION

In a recent paper (1936) by the present author, some palmate antlers from the Tung Gur formation of Mongolia were described under the name of *Stephanocemas*, and two species were assigned to this genus, *Stephanocemas thomsoni*, the generic type, and *Stephanocemas triacuminatus*. The diagnoses and distinctions of these species and of the genus were based entirely on the form of the antlers. In addition, a new species of *Dicrocerus*, *D. grangeri*, was described from a series of antlers. In a recent paper (1937), Professor H. G. Stehlin has shown that the form originally described as *Stephanocemas triacuminatus* is probably referable to the genus *Lagomeryx* Roger.

When the studies of the Tung Gur cervids were being carried on, it was thought that there were a few teeth in the American Museum collection that had been found associated with the antlers, but diligent search failed to bring these teeth to light. Recently, however, the teeth were discovered by Dr. Walter Granger while looking for some other Mongolian fossils, and he very kindly turned them over to the present author for study. They form the principal subject of this paper, because their description may throw additional light on some of the Tung Gur Cervidae.

At the same time it has been thought advisable to make some additional remarks as to the probable relationships of the genera *Stephanocemas* and *Lagomeryx*, especially in view of the recent paper by Professor Stehlin, cited above, and also of a paper on a new fauna from Tsaidam, by Dr.

Birger Bohlin, in which he describes some antlers strikingly like the Tung Gur specimens.

Cervid, cf. *Stephanocemas thomsoni*
Colbert

SPECIMENS UNDER CONSIDERATION.—Amer. Mus. No. 26772, a right mandibular ramus containing P_3 - M_3 . From the Tung Gur formation, twenty-five miles northeast of Gur Tung Khara Usu, Inner Mongolia. This is the type locality for *Stephanocemas thomsoni*.

Amer. Mus. No. 26773, fragment of a left mandibular ramus with M_2 - 3 . Horizon and locality the same as for 26772.

Amer. Mus. No. 26774, a left M^3 , much worn. Horizon and locality the same as for 26772 and 26773.

DESCRIPTION OF SPECIMENS

The teeth that form the subject of this paper were found, together with other cervid material, on a small knoll some twenty-five miles northeast of Gur Tung Khara Usu, Inner Mongolia. This is the type locality for *Stephanocemas thomsoni*, as well as for *Dicrocerus grangeri*, and it was here that paratype specimens of *Lagomeryx triacuminatus* were discovered. Thus it becomes immediately evident that the teeth to be considered below may be associated with any one of three different kinds of cervids. Before considering the question as to which of these three deer the teeth may represent, a description of the specimens will be presented.

These teeth are somewhat larger than comparable teeth of *Dicrocerus (Euprox) furcatus*, and are similar in size to the teeth of *Dicrocerus elegans*. Needless to say, the Tung Gur teeth are much larger than the teeth of the smaller species of *Lagomeryx*, such as *Lagomeryx pumilio*. As

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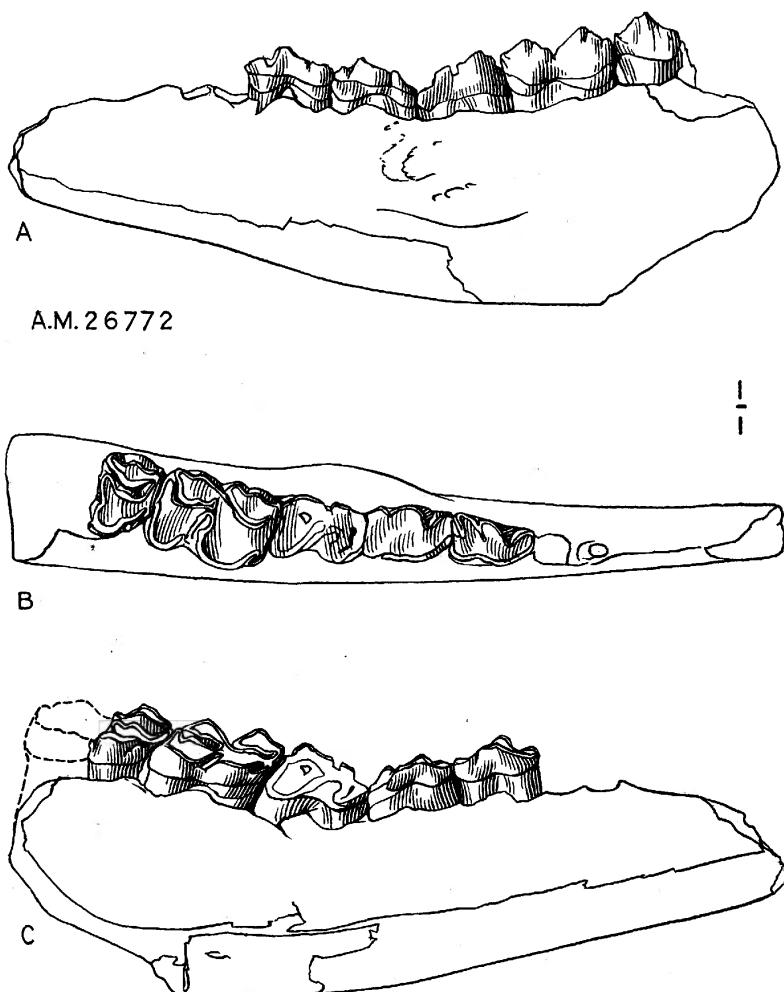


Fig. 1. Cervid, cf. *Stephanocemas thomsoni* Colbert. Amer. Mus. No. 26772, right mandibular ramus with P_3 - M_3 . A.—Internal lateral view. B.—Crown view. C.—External lateral view. All natural size.

shown by the smaller jaw fragment from the Tung Gur beds, in which the teeth are virtually unworn, the lower molars are somewhat more hypodont than the same teeth in *Dicrocerus (Euprox) furcatus* and closely comparable in this respect to those of *Dicrocerus elegans*. In this specimen the external pillars between the outer two crescents are quite small—perhaps smaller than they are in comparable teeth of *Dicrocerus*. Still another difference between the teeth from Tung Gur and those of *Dicrocerus* is to be found in the shape of the talonid of the last lower molar. In the

Tung Gur specimen, No. 26773, the continuous talonid loop is directed posteriorly, so that its mid-line is virtually parallel to the mid-line of the tooth. In *Dicrocerus (Euprox) furcatus* the talonid loop is directed outwardly, so that a mid-line drawn through it would make a sharp angle with the mid-line of the tooth. In *Dicrocerus elegans*, on the other hand, the talonid loop is directed posteriorly, as in the Tung Gur specimen, but it differs from the Mongolian specimen because its inner wall is somewhat sinuous, rather than being straight, and is interrupted in the unworn condition. The

specimens from Mongolia show a reduced *Palaeomeryx* fold on the protoconid of the molars, much smaller than the fold of *Dicrocerus (Euprox) furcatus*, and rather similar to that of *Dicrocerus elegans*. Finally, the premolar teeth of the Tung Gur deer, though worn, would seem to be on the whole like those of *Dicrocerus*, in this case probably more like those of *Dicrocerus (Euprox) furcatus*, which are short and wide, than like those of *Dicrocerus elegans*, which are elongated and transversely compressed.

Unfortunately, the single upper molar collected from the Tung Gur formation is

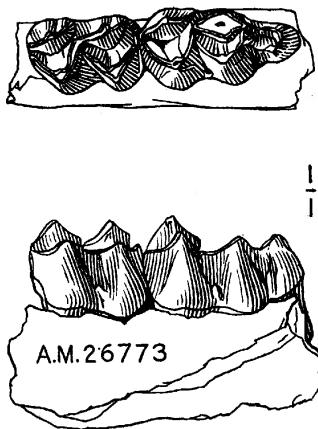


Fig. 2. Cervid, cf. *Stephanocemas thomsoni* Colbert. Amer. Mus. No. 26773, fragment of left mandibular ramus with M_2-3 . Crown view above, external lateral view below. Natural size.

very much worn, so that comparisons between it and similar teeth in other genera are indeed limited. One character of this tooth is shown to advantage, namely, the strong internal cingulum, running along the entire length of the lingual surface and curving to the anterior margin. In this respect the Tung Gur tooth differs from comparable teeth in most of the species of *Dicrocerus* and *Lagomeryx*, for in these two genera the internal cingulum usually is limited to a small, mid-valley remnant.

From this description it would seem that the teeth from the Tung Gur beds are essentially similar to teeth of *Dicrocerus*,

particularly those of the more advanced species, *Dicrocerus elegans*. Yet there are certain differences (notably the size of the internal cingulum in the upper molars and the structure of the talonid in the lower third molar) to be seen between the teeth under consideration and those of *Dicrocerus*, and also between them and the teeth of *Lagomeryx*, insofar as the dentition of this latter genus is known. The differences, though small, are probably important, since among the ruminants slight differences in the dentition are usually accompanied by marked—one might say great differences in the skull and its appendages. Because of these differences between the Tung Gur teeth and teeth of other cervuline genera of a similar geologic age, and also because the Tung Gur teeth are of a size that would correspond very well with the antlers of *Stephanocemas*, the specimens described above are hereby considered as belonging to this genus. They are also attributed to the type species, because it is the only species in the Tung Gur formation that undoubtedly may be included in this genus, and because the teeth came from the type locality for this species.

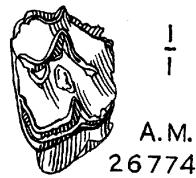


Fig. 3. Cervid, cf. *Stephanocemas thomsoni* Colbert. Amer. Mus. No. 26774, left M^3 . Crown view. Natural size.

Therefore, the dental characters of *Stephanocemas thomsoni* are at the present time to be considered as follows:

- 1.—Teeth about equal in size and hypsodonty to those of *Dicrocerus elegans*.
- 2.—Internal cingulum of upper molars strong, continuous along the lingual surface of the tooth.
- 3.—External pillars of lower molars relatively small.
- 4.—Talonid of M_3 directed posteriorly, with continuous loop.
- 5.—Remnant of *Palaeomeryx* fold on the protoconid of the lower molars.

Measurements and indices of the supposed *Stephanocemas* teeth are given below.

	A.M. 26774 LM ³	A.M. 26772 Mandible	A.M. 26773 Mandible	<i>Dicrocerus</i> <i>furcatus</i> A.M. 10353	<i>Dicrocerus</i> <i>elegans</i> A.M. 10354
M ³ l × w	13 × 18			12.5 × 14.5	
	Index	138		116	
P ₃ l × w		10.5 × 6.5		9.5 × 5.5	11.5 × 5.5
	Index	62		58	48
P ₄ l × w		11 × 7.5		9.5 × 6.5	12 × 6.5
	Index	68		68	54
M ₁ l × w		11.5 × 9			12.5 × 8.5
	Index	78			68
M ₂ l × w		14.5 × 10.5	14 × 9.5	12 × 9.5	14 × 10
	Index	73	68	79	72
M ₃ l × w		— × 11	20 × 10	18 × 8.5	21 × 10
	Index		50	47	48
M ₂ height			9.5	8	10 est.
h/l Index			68	66	72
M ₃ height		10.5		8	10 est.
h/l Index		53		45	48
w of talonid		5		6.5	5.5
w (t)/w Index		50		76	50

DISCUSSION

It might be apropos to say a few words at this place with regard to the homologies of the antlers in *Stephanocemas* and *Lagomeryx*. In the original description of the Tung Gur deer, a series of antlers of *Stephanocemas* of varying ages was described, and an attempt was made to point out the possible homologies or differences of the numerous prongs in this genus with the parts of the antler in the more typical cervids. Generally speaking, the large anterior prong of the *Stephanocemas* antler was homologized with the anterior or brow prong in the typical cervid antler, while the rest of the *Stephanocemas* antler was supposed to be more or less homologous with the posterior or beam portion of the usual deer type. In suggesting these relationships, it was supposed that the *Stephanocemas* antler is a true, definitely formed antler growth, comparable with the antlers in other deer.

Bohlin, in his description of fossil deer from the Tsaidam region of Asia, had a series of forms similar to the Mongolian fossils. This author—at that time not as yet having seen the paper on the Mongolian fossils—suggested that the prongs in the *Lagomeryx* and *Stephanocemas* types

of antler might be formed by outgrowths of the burr. Bohlin's opinion was supported in a general way by Stehlin in 1937, who thoroughly discussed the problem of homologies. This author figured a frontlet of a recent *Dama*, showing the manner in which the burr might grow out to an unusual degree (recognizing, of course, that this comparison was more in the nature of an analogy than of a true homology). It may be that this interpretation offers the valid explanation of the antler structure in *Stephanocemas*. Yet an examination of the large series of antlers from Mongolia in the American Museum collection does not seem to offer any evidence to definitely support this conclusion.

In fact, when looking over the material from the Tung Gur formation, one gets the impression that these antlers, from the beginning to the end of their ontogenetic development, are formed by the aberrant growth from characteristic prongs. That is, the large anterior prong of *Stephanocemas* certainly appears to be an homologue of the anterior prong of a *Dicrocerus* antler, while the palmate portion of the *Stephanocemas* antler, with its several lateral and posterior prongs appears to be quite defi-

nitely the result of lateral growth and "budding" from the posterior prong of a more typical cervid.

This view as to the homologies of the *Stephanocemas* antler is supported by the examination of numerous young specimens, some of which were diagrammatically figured in the previous paper on *Stephanocemas* from Mongolia. The young antlers seem to show every evidence of a derivation as outlined above, rather than by means of outgrowths from a burr.

Perhaps a satisfactory solution of this question of antler homologies and generic and specific relationships of the mid-Tertiary cervulines will of necessity have to wait until better material—especially associated antlers and dentitions, or complete skulls—is discovered.

The several types of cervulines present in the Tung Gur formation may be distinguished as follows:

1. *Stephanocemas*.—A form having a complex, palmate antler borne on a relatively short pedicle. *Stephanocemas thomsoni*, the characteristic Tung Gur species, is the type of the genus.

2. *Lagomeryx*.—A form in which the antler is, in the Tung Gur species, characterized by three tines, radiating from the top of an elongated pedicle. *Lagomeryx triacuminatus*, the Tung Gur form, was originally described as a species of *Stephanocemas*.

3. *Dicrocerus*.—There are two *Dicrocerus* types in the Tung Gur fauna. *Dicrocerus grangeri* would seem to be a true *Dicrocerus*, in the restricted sense of the term, characterized by the two prongs branching from the burr direct and somewhat separate from each other. The other *Dicrocerus* type from the Tung Gur beds was originally described as *Dicrocerus* sp., but according to the restricted usage as defined by Stehlin, should be referred to the genus below.

4. *Euprox*.—A *Dicrocerus* type of cervuline in which the fork of the antler arises at some distance above the burr, which latter structure is well developed.

It may be well to compare these types with related forms from other parts of Eurasia.

Stephanocemas thomsoni is closely comparable to the European species *Stephanocemas elegantulus* (Roger) as recently described and illustrated by Stehlin in his very valuable paper dealing with *Stephanocemas* and *Lagomeryx* (1937). The Mongolian and European species, at least as

judged from their antlers, must be closely related to each other. The Mongolian form is likewise related to *Stephanocemas* sp. as described by Bohlin from the Tsaidam, and less closely connected to the Shantung species, *Stephanocemas colberti*, recently described by Young. Unfortunately these last two species are known from very fragmentary material.

The Mongolian *Lagomeryx* is a very large species of the genus, and of the several European species, only *Lagomeryx praestans* from Chitenay, recently described by Stehlin, approaches it in size. In this respect the Mongolian species may be compared with *Lagomeryx tsaidamensis*, to which form, as well as to the Chitenay species, it must be rather closely related.

Dicrocerus grangeri is a rather peculiar species of this genus, if it is properly referable to *Dicrocerus*. In a way, it looks like some of the specimens of *Stephanocemas elegantulus*, yet the large series of antlers from Mongolia show, if anything, that this "*Dicrocerus*" type of antler is quite distinct from the typical *Stephanocemas thomsoni*, of which species there is a complete age series. In the Augsburg material, described by Stehlin, there would seem to be somewhat of a gradation between an antler similar to that of *Dicrocerus grangeri* and the characteristic *Stephanocemas* antler. Yet in the Mongolian material such a gradation does not appear. Therefore, for the time being, it would seem advisable to continue to regard these *Dicrocerus grangeri* antlers as referable to the genus *Dicrocerus*, particularly in the restricted sense as it was defined by Stehlin.

The *Dicrocerus* sp. from the Tung Gur is comparable to the European *Euprox furcatus*, or to *Dicrocerus* sp., described by Bohlin from the Tsaidam.

Stehlin has suggested that the middle Tertiary cervulines originated for the most part in central Asia, migrating from there to Europe. With regard to the origin and migrations of the Palaearctic cervulines two facts are of interest. One is that the Asiatic forms are as late in geologic age, or later than the European forms. The other is that, for the most part, the

Asiatic species are larger and more "advanced" than the European types. Yet these facts may not militate against Stehlin's suggestion. Rather they may be in line with the theory, forwarded some years ago by Matthew, that advanced species develop at the place of origin of a phylogenetic line, and by their evolution push the primitive types toward the periphery

of the distribution area. Thus, we might expect to find the large, advanced species in central Asia, near the center of origin, while the small, more primitive species would be found in outlying areas, such as Europe.

The geologic relationships of certain Palaearctic cervulinines are shown by the accompanying diagram.

	Europe	Asia
Pontian		Tsaidam
Sarmatian		<i>Stephanocemas</i> sp. <i>Lagomeryx tsaidamensis</i>
Vindobonian	Stätzling <i>Stephanocemas elegantulus</i> <i>Lagomeryx meyeri</i> , etc. Sansan <i>Dicroiderces elegans</i>	Tung Gur <i>Stephanocemas thomsoni</i> <i>Lagomeryx triacuminatus</i> <i>Dicroiderces grangeri</i> Shantung <i>Stephanocemas colberti</i> <small>[<i>Heterocemas simpsoni</i>—cervid?]</small>
Burdigalian	Chitenay <i>Lagomeryx praestans</i>	

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